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POTATO LEAF ROLL AND ITS INSECT VECTORS
IN THE EDMONTON DISTRICT

Thomas Ralph Davidson
Department of Entomology

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POTATO LEAF ROLL AND ITS INSECT VECTORS

IN THE EDMONTON DISTRICT

The undersigned hereby certify that they have read and recommend to the Committee on Graduate Studies for acceptance the following thesis on "Potato Leaf Roll and Its Insect Vectors in the Edmonton District", submitted by Thomas Ralph Davidson, B.Sc. in Agriculture, in partial fulfilment of the requirements for the degree of Master of Science.

UNIVERSITY OF ALBERTA

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IN THE EDMONTON DISTRICT

Thomas Ralph Davidson
Department of Entomology

A THESIS

submitted to the University of Alberta in
partial fulfilment of the requirements for
the degree of
MASTER OF SCIENCE

Edmonton, Alberta

April, 1945

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POTATO LEAF ROLL AND ITS INSECT VECTORS

IN THE EDMONTON DISTRICT

Thomas Ralph Davidson

INTRODUCTION

Leaf roll is a virus disease of potatoes which is becoming more and more prevalent in Alberta. This disease, like many others in this category, is transmitted by aphids, those tiny insects commonly called plant lice. The first purpose of the project outlined in this thesis was to determine if any of the aphid species, which have been proved to be leaf-roll vectors, are present in the Edmonton district, and, if so, what is their relative abundance.

One of the interesting symptoms of the disease is the appearance of tuber phloem necrosis. This necrosis appears only in the year of infection, and, since the aphid is practically the only vector of the virus under natural conditions, it is only reasonable to conclude that some relationship exists here. The second purpose of this project was to determine what relationship, if any, does exist between the aphid vector, the leaf-roll virus, and the appearance of tuber phloem necrosis.

Historical Review

Leaf roll is one of the so-called "degeneration" diseases of potatoes. Although no definite proof can be obtained, this disease was probably widespread in Europe as early as 1770 (31). Leaf roll was first recognized as a specific disease in Germany and Denmark in 1905. Two years later a general outbreak occurred in the former country. This marked the beginning of extensive scientific study of the disease. In 1911 an outbreak occurred in northern Colorado and western Nebraska. Quanjer (55), in 1913, proved that phloem necrosis of the stem is a constant internal symptom of leaf-roll infected plants. This was verified by Artschwager (2) in 1918. The first extensive report on leaf roll in America was published by Orton (48) in 1914. In this work he brought together all the information available on the subject at the time. He stated that, "The literature on leaf roll has become so voluminous that few will undertake to peruse all the contributions, which are, indeed, of very uneven merit, and anyone who attempts it is likely to emerge with his concepts of the disease more confused and hazy than at the start." In 1916, Quanjer et al (57) proved that the virus could be transmitted from a diseased to a healthy plant by vine grafting. Transmission of the virus by aphids was proved by Botjes (9) in 1920, and by Schultz and Folsom (63) in 1921. In the same year Schultz and Folsom (63) noted the common occurrence of tuber phloem (net) necrosis and hair sprout in relation to the presence of the leaf-roll virus. In 1923, Quanjer (56) demonstrated that in the case of aphid transmission, particularly if this occurs late in the season, the first season's symptoms may not develop on the above-ground parts of the plant. During recent years a tremendous

1. Introduction

The purpose of this study is to investigate the effects of various factors on the growth and development of the human body.

The study was conducted over a period of 12 months, during which time data was collected from a sample of 100 individuals.

The sample was divided into two groups: a control group and an experimental group. The control group consisted of 50 individuals, while the experimental group consisted of 50 individuals.

The experimental group was subjected to a series of interventions designed to manipulate the growth and development of the human body.

The interventions included changes in diet, exercise, and environmental factors. The control group was not subjected to these interventions.

The data collected from the experimental group was compared to the data collected from the control group. The results of the study are presented in the following sections.

The first section of the study is a review of the literature. This section discusses the current state of knowledge regarding the growth and development of the human body.

The second section of the study is a description of the methods used in the study. This section discusses the sample, the interventions, and the data collection procedures.

The third section of the study is a presentation of the results. This section discusses the findings of the study, including the effects of the interventions on the growth and development of the human body.

The fourth section of the study is a discussion of the results. This section discusses the implications of the findings and the limitations of the study.

The fifth section of the study is a conclusion. This section summarizes the findings of the study and provides recommendations for future research.

The sixth section of the study is a bibliography. This section lists the sources of information used in the study.

The seventh section of the study is an appendix. This section contains additional information related to the study, including raw data and detailed descriptions of the interventions.

The eighth section of the study is a list of figures. This section contains a list of the figures included in the study, along with brief descriptions of each figure.

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amount of work has been done on this disease, which is now recognized as one of the most important virus diseases of the potato.

Distribution

General

Information as to the exact distribution of leaf roll is limited. However, it is safe to say that the virus is present in every potato-growing country today, although certain limited areas are still apparently free. Naturally, the disease is most severe in those areas where its aphid vectors are plentiful.

Local

In Alberta leaf roll is becoming more and more general. Naturally enough it is far more common in and about the cities and larger towns than it is in the country. There are a number of reasons for this, the main one being the crowding together of small plots on vacant lots. Such conditions are ideal for the spread of this disease by its principal insect vectors, the aphids. This situation has been greatly aggravated during recent years by the tremendous increase in the number of victory gardens. Generally, too, the small gardener keeps his own stock for seed, in many cases using small tubers for this purpose. As will be seen later, this is only asking for trouble, because such tubers are far more likely to be infected than are those of normal size. According to Sanford (59), nearly all the potato fields in and near Edmonton are infected with leaf roll. In many cases 50% or more of the plants suffer from the disease. Such a prevalence of the virus can only mean a considerable yearly loss to the gardener. In

the country, fields are far apart and if the seed is free from leaf roll to begin with it has a good chance of remaining so for some time at least. Nevertheless care should always be taken, as this disease will render stock valueless in three to four years.

Economic Importance

An idea of the extreme destructiveness of this disease can be gained from a statement made by Murphy (43), "There are few diseases which exert a more disastrous effect on the potato or reduce the yield more than leaf roll." As indicated by this statement, the reduction in yield in any one year by this virus alone may be extremely heavy. The following table, taken partly from Gardner and Kendrick (25) and partly from original works, as indicated, gives us some indication of the losses experienced in various parts of the world.

Table 1. Percentage reduction in yield of potatoes due to leaf roll in various parts of the world.

Authority	Country	Reduction in yield %
Murphy (43)	Canada	66 - 82
Murphy	Ireland	59 - 79
Schultz and Folsom (63)	Maine	42
Hungerford	Idaho	80
Cotton	Great Britain	36 - 75
Whitehead (76)	Ireland	45 - 79
Whitehead (76)	Wales	45 - 56
Gram	Denmark	20 - 89
Wortley (77)	Bermuda	60 - 80
Gardner and Kendrick (25)	Indiana	22 - 86
# Bonde <u>et al</u> (8)	Maine	0 - 100

Nineteen year period.

Apart from reduction in yield, leaf roll causes a further loss. Tubers from infected plants are usually very small and are of little or no marketable value. This is true mainly in the case of secondary leaf roll, as there is little reduction in yield from primary infection. In these cases of primary infection, where reduction in size of tubers is not so general, the appearance of necrotic tubers reduces the marketability to a considerable degree.

Since this disease is present in all the main potato growing areas, conditions are ideal for its continued dissemination. This is especially true in seed growing areas where the insect vectors of the virus are abundant. The necessity of having rigid control measures to overcome this menace is, therefore, evident.

Symptoms of Leaf Roll

(General references 23, 32, 31, 43, 78)

Rolling of the Leaves

As the name suggests, one of the most common characteristics of the disease is the rolling of the leaves. The margins curl upwards and inwards towards the midrib. The cause of rolling is described by Murphy (44) as follows; "The accumulation of carbohydrates in the leaf tissue results in an abnormal distension of the spongy, as compared with palisade parenchyma and since this swelling is unimpeded except in the direction of the more rigid palisade cells on its upper side, one of the results is the upward rolling of the margins of the leaflets."

Generally rolling begins at the apical end of the leaf, nevertheless it is not uncommon to see the basal areas curled first. It must be kept in mind here that apart from leaf roll there are a number

of diseases and nutritional disorders which cause leaf rolling very similar if not identical to that produced by the leaf-roll virus itself. It should also be remembered that, due to climatic conditions or other factors, symptoms may be partially or entirely masked or suppressed. In cases where infection occurs late in the season rolling of the leaves may not occur or it may be confined to the upper portion of the plant. However, if infection has occurred early or has resulted from a diseased seedpiece, rolling will begin on the lower leaves and gradually affect the entire plant. (See Figs. I and II.)

Rigidity

The leaves of an infected plant feel hard and leathery. They are very brittle and crack rather than bend. According to Wortley (77) leaves thus affected "do not wilt and become limp during drought as normal leaves do." This rigidity is due to an accumulation of starch in the petioles and lamina of the leaves. This point of starch accumulation will be discussed in more detail later.

Foliage Colour

Foliage colour is not a character which can be used to any great degree of accuracy in diagnosis. This is due to the fact that the discolouration depends to a great extent on the variety affected, climatic conditions, and severity of infection. Generally there is a slight yellowish tinge to the affected leaves, but some varieties show a reddish or purplish discolouration. Varieties such as Green Mountain, Carter's Early Favourite, and Netted Gem have little pigment in their cells and hence may exhibit a yellowish colour when affected. The

of course a very important factor in the
analysis of the situation is the fact that
the situation is not static but is in a
constant state of flux. It is therefore
essential to have a clear understanding of
the factors which are influencing the
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FIGURE I

A potato plant showing symptoms characteristic
of severe leaf roll



FIGURE II

A unit of leaf-roll infected potatoes
in the field



of foliage/highly pigmented varieties such as Warba and Early Ohio develops a reddish tinge. In most cases these colour symptoms become more definite late in the season.

Type of Growth

In cases of primary infection there may be little or no change in growth form, especially in those cases where infection occurs late. If, however, infection has occurred very early, the plant may appear more erect than normal, due to the shorter angle between the petioles and the stalk. However, this is not a constant character, and cannot be depended upon. Where infection is secondary, plants are usually much dwarfed and shorter-lived. Often they show erectness as described above, but on the other hand affected plants may be so weak as to be recumbent.

Phloem Necrosis of the Stem

Attention was first drawn to this symptom by Quanjér (55). His work was confirmed by Artschwager (2), who described it as a constant internal character. Later, in 1923, Artschwager (3) stated that, "Stem sections of a typical leaf-roll plant exhibit, as a diagnostic internal symptom, a necrosis and lignification of the phloëm groups. In the case of severe external symptoms, the diseased groups pervade the entire plant, with the occasional exception of the underground organs. The distal stem region is commonly affected, and in nearly every instance the necrotic changes are of an extreme type. The basal stem region always shows necrotic changes when external symptoms become evident while the plant is still young. As a rule, necrosis of the phloëm in the lower stem means generally necrosis of the plant

throughout its extent, but the symptoms may decrease towards the distal end or disappear altogether. At any given height of the stem, the node is typically more severely affected than is the internode. This condition is especially observed in the initial stages of the disease, but during subsequent development either region may be equally affected While obliteration of the phloem is always observed in connection with leaf roll it is also an accompanying phenomenon in other diseases. It is not so much its mere presence as its universality in distribution, coupled with the absence of necrosis in other tissues, which gives it a real diagnostic value." Discoloration is due to the lignification and later destruction of part or all of the primary phloem. Following the breakdown of the cells, the space is filled with a dark gummy substance. Artschwager (3) and Sheffield (64) both emphasize the fact that only the phloem is thus affected.

Starch Accumulation

In normal plants the starch which is stored up in the leaves during the day is removed at night. However, in leaf-roll infected plants, due to the stoppage of the phloem tissues, this translocation is not complete. A simple iodine test will reveal the presence of starch in the leaves in the morning. Barton-Wright and McBain (4) did a great deal of work in determining the cause of this accumulation of starch. A brief review of their work will be of value here. Looking first at the normal plant, it was found that photosynthesis results in the production of hexoses. During periods of high light intensity, normal daylight, the hexose is converted to sucrose. This is a somewhat reversible reaction. Due to the rapidity of the forward reaction

the sucrose becomes too concentrated for rapid removal. This results in the condensation of hexose to starch, also a reversible reaction (Fig. III). During the night, or under conditions of low light intensity, there is still a hexose to sucrose reaction and at the same time a hydrolysis of starch to sucrose (reversible), which is removed to other parts of the plant, principally the tubers (Fig. IV).

In a leaf-roll infected plant, due to the partial destruction of the phloem, sucrose cannot readily be removed. Hence, there is an accumulation of this sugar, the result being the conversion of sucrose to starch. There is at the same time the condensation of hexose to starch as before. Hence, there are three reversible reactions in a closed system, thus - starch to hexose, hexose to sucrose, sucrose to starch (Fig. V). Now, "according to the law of mass action, chemical action diminishes as the products of activity accumulate; the initial rate can only be maintained provided the initial concentrations of the reacting substances are provided and the products of the reaction removed." (4). This probably explains the low rate of photosynthesis that is common to leaf-roll infected plants.

Spindling Sprout or Hair Sprout

Leaf-roll infected tubers may produce very small, weak, spindly sprouts. This, however, is not a constant character, and, therefore, is of little diagnostic value. It should be noted here that spindling sprout always arises from that part of the tuber showing phloem necrosis (23). The reason for this is quite evident. The conducting channels in this portion of the tuber have been plugged or destroyed. Thus the movement of food material is greatly inhibited or prevented and the sprout suffers from starvation.

FIGURE III

Reactions in a normal plant by day (diagramatic)^a

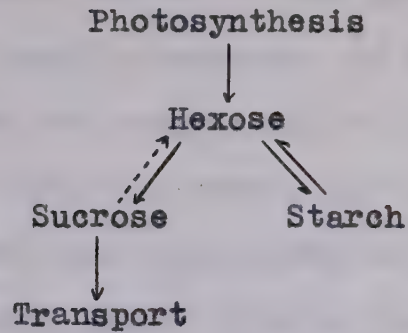


FIGURE IV

Reactions in a normal plant by night (diagramatic)^a

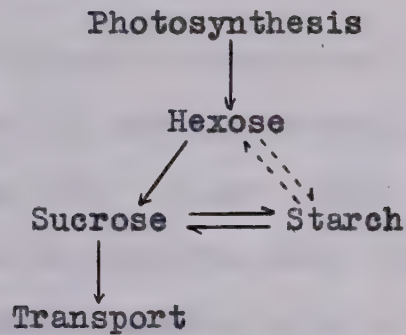
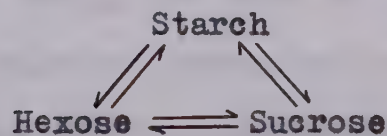


FIGURE V

Reaction in a leaf-roll infected plant (diagramatic)^a



a. After Barton-Wright and McBain.(4).

Persistence of the Seed Piece

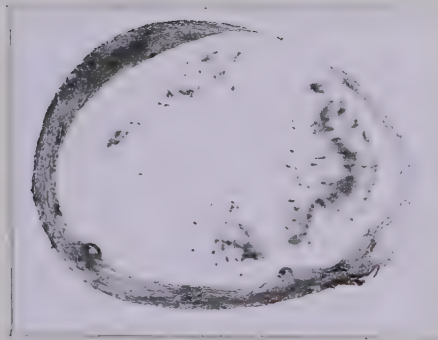
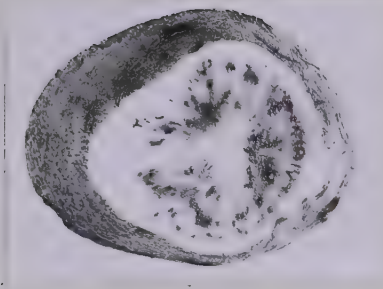
In the case of disease-free material, the seed piece (set) generally decomposes before the end of the growing season. However, leaf-roll infected sets usually persist. In an attempt to explain this, McLean (41) studied the composition of diseased and healthy mother tubers. He found that the percentage of dry matter was higher in leaf-roll mother tubers than in healthy mother tubers. It is concluded that the leaf-roll plant derives very little nutrient from the set. Healthy plants, however, rapidly use up the nutrient material in the mother tuber.

Net or Phloem Necrosis of the Tuber

Net necrosis of the tuber is described by Schultz and Folsom (63) as being, "a discoloration of the fibrovascular bundles originating at the rhizome scar" (Fig. 6). It may extend over the entire tuber, but is generally confined to the stem end. Again, according to Schultz and Folsom (63), "net necrosis appears more often as conditions of variety, recency of infection and weight of tuber are more favourable". It may develop in the dormant tubers without relation to differences in the storage temperature. Folsom et al (23) reported that this net necrosis can develop only during the year of primary infection. This again, however, is not a constant character and may or may not appear. Work by Sanford and Grimble (60) confirmed these observations. These writers also report an indistinguishable phloem necrosis, non-virus in nature, which is produced by the tomato psyllid, Paratrioza cockerelli Sule. feeding on the potato vines. They put forth the theory that tuber phloem necrosis in the case of leaf roll may also be caused by the

FIGURE VI

Cross-sections of a tuber showing
phloem necrosis



insect vector of the disease rather than by the virus, or that it may be a result of the combined effect of the insect and virus. As will be indicated later, the present problem is based upon this hypothesis.

Reduction in Tuber Size

A further characteristic which is quite constant in cases of secondary leaf roll is the great reduction in the size of the tubers. Affected plants tend to produce an abnormally large number of small tubers. This tendency becomes more pronounced every year. Actually, the total tuber mass may not be greatly reduced for a year or two after infection. If, however, the same material is used for five or six years the ultimate result is a clump of very small tubers which are valueless. The reason for this is purely physiological. Phloem necrosis of the stem results in a starving effect. The normal tendency of any plant under such conditions, no matter what the cause, is to send out more and more branches. This only aggravates the situation, making the plant weaker than before, and it finally dies.

The symptoms described here are those typical of leaf roll wherever it is found. An upright habit, stiff, leathery leaves rolled upwards at the margin are characteristic symptoms of secondary leaf roll. Symptoms due to initial infection are less pronounced and the foliage may have a yellowish or reddish tinge. Tubers produced by plants suffering from secondary infection are generally small and numerous, while those produced by plants with primary leaf roll, though often normal in size, may show phloem necrosis.

Nature of Viruses

One of the questions which comes to mind when studying a disease of this sort is, "What is a virus?" To date this question has not been answered satisfactorily. The causal agent is an infectious property so small that it cannot be seen with the ordinary microscope; it passes readily through ordinary bacteria-proof filters; and it cannot multiply in the absence of the living host cells. Of the many theories presented four will be referred to at this time. (See Heald (32, 31), and Smith (69).)

Bacterial Theory

Virus diseases do behave in many respects like known bacterial diseases. Because of this, and the fact that bacteria are often found associated with virus infected plants, many workers considered them to be bacterial in nature. Recent work, however, has shown that the presence of bacteria is purely secondary and that disease can be produced by bacteria-free plant juice. This practically eliminates the possibilities of this theory.

Enzyme Theory

Viruses show a number of characteristics which are identical with those exhibited by enzymes. According to Heald (31) they are absorbed by talc as are enzymes; they show specific reactions with formaldehyde; they are resistant to numerous antiseptic substances; they are destroyed by concentrations of alcohol that inactivate enzymes; and they are denatured by temperatures that inactivate enzymes. According to this theory, a very small amount of the enzyme, once introduced into the

living host tissue, can, in some way, catalyze its own production. This theory is, however, no longer accepted.

Protozoan Theory

Many workers found, in the cells of virus infected plants, inclusion bodies which they believed to be amoeboid or protozoan in nature. It was thought that they were a stage in the life cycle of the organism. It is now believed, however, that these bodies are caused by the derangement of the cells which always accompanies virus infection.

Filterable Virus Theory

The term "virus" is used here to refer to those filterable agents or principles which have the power of producing disease. As to the exact nature of these viruses, four theories have been presented in the past. These are: (1) A non-corpuseular, water-soluble substance. It is now known that a virus is a definite particle. (2) A very minute, bacteria-like organism. The extremely small size makes this theory hard to accept. (3) A chemical substance of unknown nature but with the ability to reproduce. Recent investigation has proved that viruses are protein in nature. (4) An infectious, crystalline protein. Scientists have proved that viruses are proteins, the exact nature of which is not yet completely understood. They are of a very complex type similar to nucleoproteins.

Physical and Chemical Properties of Virus Proteins

In order to understand these substances better, consideration is now given to the various physical and chemical properties of virus proteins.

Temperature

All viruses tested to date are readily destroyed by heat, although there is a fairly wide temperature range in their thermal death points. For the viruses studied in detail up to the present time, inactivation occurs between 40° and 90° C. The thermal death point for a number of viruses is given below in Table 2.

Table 2. Thermal death points of some virus proteins.

Virus	Reference	Thermal death point, °C.	Time minutes
Tobacco mosaic	37	90	10
Tobacco spot mosaic	37	65	10
Mottle of potato	69	66	10
Tobacco mottle necrosis	37	70	10
Aucuba mosaic of potato	34	65	10
Cucumber mosaic	37	70	10
Rugose mosaic of potato	36	60 - 65	
Veinbanding of potato	40	60	
Marginal leaf-roll of potato	34	60 - 65	10
Ring-spot of potato	40	68	
Potato virus Y	69	52	10
Crinkle mosaic of potato	36	43 - 45	
Mild mosaic of potato	36	40 - 45	
Leaf-rolling mosaic	36	70 - 75	

According to Stanley and Loring (73) the cause of inactivation is due to a splitting of the protein into at least two portions. The nucleic acid portion separates and remains soluble while the remainder

of the protein precipitates out in neutral solution. Stanley and Loring (73) go on to say that similar results are obtained where the virus is denatured by means of certain acids or alkalies.

Effect of Drying on Longevity

The length of life of virus proteins either in dried plant tissue or in vitro, extracted plant juice, also varies over a wide range. Some viruses such as tobacco mosaic are very resistant to desiccation in dried plant tissue, while others are inactivated almost immediately. Longevity seems to depend to some extent on the host. Burnett (10) found that latent virus was still infective after being dried for 286 days in tobacco tissue, 263 days in potato tissue, but not over 50 days in tomato tissue. Similarly, the veinbanding virus of potatoes was viable after drying for 50 days in potato and tobacco, but for only 17 days in tomato. This, as well as showing the effect of host tissue, also demonstrates extreme variability between viruses themselves. According to Stanley and Loring (73), "The same relationship exists between the relative stabilities of the purified virus solutions as between the relative stabilities of the crude infectious tissue extracts." He states that tobacco mosaic can be kept in a sterile filtrate at room temperature for a number of years; latent mosaic of potatoes for six months; and tobacco ring spot for only a day at the most. Longevity in vitro of crinkle mosaic, one to two days; rugose mosaic, one to two days; mild mosaic, two to four hours; and leaf-rolling mosaic, one to two days (36). Longevity is here affected to some extent by the temperature of storage. Smith (69) found that potato virus Y will remain active for only 48 hours in sap extract at room temperature, while it will remain viable for 141 days at -10° C.

Pressure

Another property, which has not as yet been very closely studied, is the pressure death point, which, for those viruses tested, has been found to be very high. According to Gidding et al (26) a pressure of 130,000 pounds was required to inactivate tobacco mosaic. This is higher than that required to kill many bacteria, but lower than that for Bacillus subtilis. It will also be noted that this is a greater pressure than that required to inactivate certain enzymes but is approximately on a par with pepsin.

Dilution

A further property of viruses is their infectivity at rather high dilutions. Here again, however, there is a very wide range of variation. At the top of the list is tobacco mosaic, which is infective in dilutions of 1:1,000,000 (37), while potato crinkle mosaic, at the other end of the scale, is non-infective at dilutions of 1:100 or even less.

Filterability

The size and shape of virus particles has been derived by various methods, such as filterability, molecular weight and density, electron microscope, etc. These methods, on the whole, give relatively the same results. The sizes of six viruses, as determined by these various methods, are given in Table 3.

Table 3. Size of virus particles as determined by various methods.

Virus	Reference	Size (microns) ^{milli-}
Potato latent mosaic	73	9.8 x 430
Tobacco latent mosaic	71	10 x 400
Tobacco mosaic	72	15 x 200
" "	33	15 x 200
" "	71	15 x 330
" "	73	12 x 430
Tomato bushy stunt	71	27.4, spherical
" " "	72	26 , "
" " "	33	26 , "
Tobacco ring spot	71	19, spherical
Tobacco necrosis	72	20, spherical
" "	33	20, "

From the above figures it is seen that the various authors do not always agree, but variations are relatively small and may be due to experimental error or the method of determination employed. It can also be seen from the above that while certain virus particles are spherical others are rectangular in shape. These latter are not necessarily symmetrical. That is, the particles may be larger at one end than the other.

Molecular Weight

It might be well at this point to note the extremely high molecular weight of virus proteins.

Table 1. Summary of data for the first 1000 cases.		
Case No.	Age (years)	Sex
1	25	M
2	30	F
3	35	M
4	40	F
5	45	M
6	50	F
7	55	M
8	60	F
9	65	M
10	70	F
11	75	M
12	80	F
13	85	M
14	90	F
15	95	M
16	100	F
17	105	M
18	110	F
19	115	M
20	120	F
21	125	M
22	130	F
23	135	M
24	140	F
25	145	M
26	150	F
27	155	M
28	160	F
29	165	M
30	170	F
31	175	M
32	180	F
33	185	M
34	190	F
35	195	M
36	200	F
37	205	M
38	210	F
39	215	M
40	220	F
41	225	M
42	230	F
43	235	M
44	240	F
45	245	M
46	250	F
47	255	M
48	260	F
49	265	M
50	270	F
51	275	M
52	280	F
53	285	M
54	290	F
55	295	M
56	300	F
57	305	M
58	310	F
59	315	M
60	320	F
61	325	M
62	330	F
63	335	M
64	340	F
65	345	M
66	350	F
67	355	M
68	360	F
69	365	M
70	370	F
71	375	M
72	380	F
73	385	M
74	390	F
75	395	M
76	400	F
77	405	M
78	410	F
79	415	M
80	420	F
81	425	M
82	430	F
83	435	M
84	440	F
85	445	M
86	450	F
87	455	M
88	460	F
89	465	M
90	470	F
91	475	M
92	480	F
93	485	M
94	490	F
95	495	M
96	500	F
97	505	M
98	510	F
99	515	M
100	520	F

The data presented in Table 1 show the distribution of ages and sexes for the first 1000 cases. The ages range from 25 to 520 years, with a median age of approximately 150 years. The distribution is roughly equal between males and females, with a slight excess of males in the younger age groups and a slight excess of females in the older age groups. The data suggest that the incidence of the disease is relatively low in the younger age groups and increases with age, particularly in the older age groups.

The data presented in Table 2 show the distribution of ages and sexes for the next 1000 cases. The ages range from 25 to 520 years, with a median age of approximately 150 years. The distribution is roughly equal between males and females, with a slight excess of males in the younger age groups and a slight excess of females in the older age groups. The data suggest that the incidence of the disease is relatively low in the younger age groups and increases with age, particularly in the older age groups.

Table 4. Molecular weight of virus proteins.

<u>Virus</u>	<u>Reference</u>	<u>Molecular weight</u>
Tobacco mosaic	71	50,000,000
Tobacco latent mosaic	71	26,000,000
Tobacco ring spot	71	3,400,000
Tomato bushy stunt	71	8,800,000
Tobacco necrosis	71	7,400,000
Potato latent mosaic	73	30,000,000
Cucumber mosaic	73	43,000,000

Effect of Chemicals

Still another property which should be considered here is the effect of chemicals on the virus protein. Smith (69) and others found that certain viruses were quite resistant to the action of glycerine. This is not the case with bacteria. Allard (1) lists a number of chemicals which he found to have little or no effect on viruses. Acetone, nitric, hydrochloric, phosphoric, citric, acetic and carboic acids, sodium carbonate, manganese sulphate, sodium chloride, aluminium sulphate, lead nitrate, lithium nitrate, sodium nitrate, silver nitrate, mercuric chloride were mentioned. Two substances which quickly destroy virus proteins are 80 per cent ethyl alcohol and 40 per cent formalin. Although there is considerable variation between the various viruses they are, as a group, relatively resistant to chemical agents.

Chemical Structure

In regard to the chemical structure of virus proteins, only preliminary work has been done. However, Stanley and Loring (73) state that the nitrogen content is about that usually given for proteins. Viruses are not, however, simple proteins. They are, on the other

hand, at least as complex as the nucleo-proteins. As demonstrated by Pirie, they contain nucleic acid and probably other substances. Stanley and Loring (73) state that, "The nature of the combination of protein and nucleic acid is not known, but the two appear to be in relatively stable combination, for they are not separated by dialysis against water at pH 8 or by repeated sedimentation, which has been demonstrated to separate mixtures of virus protein and virus nucleic acid." Below is a table showing the analysis of purified virus proteins as presented by Stanley and Loring (73) (Table 5).

Table 5. The chemical composition of certain virus proteins.

Virus	Carbon %	Hydrogen %	Nitrogen %	Sulphur %	Phosphorus %	Carbo- hydrate as glucose %	Nitrogen : Phosphorus	Carbo- hydrate : phosphorus
Tobacco mosaic	49.3- 50	7.2- 7.4	14.4- 16.6	.24- .59	.45- .55	2.5	26-37 :1	4.6-5.6 :1
Aucuba mosaic	49.1- 50.5	6.6- 6.9	16.5- 16.8	.24	.51		32-33 :1	
Cucumber mosaic	50 - 51	7.1- 7.6	15.3- 15.8	0-0.6	.55- .66	2.2- 2.5	26-29 :1	3.7-4.6 :1
Latent mosaic	47.7- 49.5	7.1- 7.7	15.7- 17.0	1.1	.4- .5	2.5- 3.0	31-43 :1	5.0-7.5 :1
Tobacco ring spot	50.5	7.3- 7.8	14.3- 14.9	0.39	1.6- 1.8		8 - 9 :1	
Tobacco bushy stunt	47- 50	7.2- 8.2	15.8- 16.4	0.4- 0.8	1.3- 1.5	5-6	11-13 :1	3.3-4.6 :1

As will be seen from this table, the percentages of carbon, hydrogen and nitrogen vary relatively little. The approximate percentages are: carbon, 50, hydrogen, 7.5; nitrogen, 16. The percentages of

these elements cannot therefore be used as diagnostic characters. The amounts of sulphur and phosphorus, although small, vary over a relatively greater range and are fairly constant for a given virus. Stanley (71) gives this range as 0.2 - 2.2% for sulphur, and 0.5 - 4.1% for phosphorus. The exact value of this in classification is not yet known.

Relatively little work has been done on the complete chemical analysis of virus proteins. Most research to date has been with the tobacco mosaic virus. According to Hoagland (33), 68% of the constituents are now known. He lists the following amino acids as being present:

tryosine	3.8%	aspartic acid	2.4%	serine	6.4%
arginine	9.0%	valine	3.9%	glutamic acid	6.3%
proline	4.7%	phenylalanine	6.0%	leucine	6.1%
threonine	5.3%	tryptophane	4.5%	alanine	2.4%

Glycine and histidine appear to be absent. Although this does not agree exactly with Stanley's work, the differences are not great. As to what makes up the remaining 22% no one knows at present. However, the above indicates the extremely complex nature of these proteins.

Transmission of Viruses

Virus diseases are of an extremely infectious nature. Here again, however, there is a great deal of variation within the group, and, consequently, they are transmissible by various means. The main methods of transmission, both natural and artificial, are briefly discussed below.

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Grafting

This is a method by which all viruses can be transmitted. In certain cases it seems to be the only method of dissemination. Grafting consists of an organic union between the scion from diseased material and the healthy stock. All methods of grafting usually employed by horticulturists and others are equally effective in spreading these diseases. Methods of tuber grafting, in which portions of diseased tubers are brought in contact with healthy tubers, have been employed in the study of potato diseases. Transmission is readily obtained. Grafting is, of course, an artificial means of transmission, but since it is a practice used widely in the propagation of many plants we cannot afford to overlook its importance.

Inoculation

This is also an artificial method of transmission, in which the express juice of a virus-infected plant is, by one means or another, applied to a healthy plant. As far as is known, a wound of some kind is always necessary. However, due to the extreme infectiousness of certain of the viruses, such as those of the mosaic type, the breaking of a trichome is sufficient. Generally the wound, if it is of a small nature, has to be made in the immediate presence of the virus. The economic significance is immediately understood if one considers the normal methods used in pruning. Certain of the more infectious viruses can be carried on the pruning knife from diseased to healthy plants. The mere handling of a healthy plant after a diseased one is, in some cases, sufficient for transmission.

Seed

Generally speaking, viruses are not transmitted by the seed. There are, however, a few exceptions. Mosaic of certain of our legumes is known to be perpetuated in this manner. Pierce (54) found that the mosaic of the common bean was viable in the bean seed for thirty years. Lettuce mosaic (47) is also transmissible by the seed. A few others have been definitely proved to be disseminated by this means, for example, soy-bean mosaic (39), squash mosaic (42), and muskmelon mosaic (38). Apart from these, still others are strongly suspected. It may be that this is a more important means of transmission than has thus far been proved to be the case.

Contact of Foliage or Roots

Transmission by leaf or stem contact is naturally limited. Dissemination of this type occurs most readily during storms, when wounds, which are necessary for entrance of the virus, are most likely to be produced. Transmission by root contact is probably less common than that of foliage contact.

Pollen

Although transmission by this means has been reported on two occasions and has been suggested, at certain other times, no definite information is available. It is possible that pollen transmission is of more importance than has been suspected to date.

Insects

Insects are probably the most important means of virus transmission

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in the field. It is true that insect vectors have not been found for all virus diseases, and probably do not occur for a few, but the majority of viruses are disseminated in this way. In some cases it is purely mechanical transmission, but, on the other hand, there is often a very specific and biological relationship. In such cases the vector may transmit only one virus and exhibit a selective power in this regard. Often the virus remains viable in the body of the insect throughout the life of the vector.

Parasitic Seed Plants

Transmission of viruses by means of dodder has been proved by Johnson (35). No estimate as to the importance of this method of dissemination can be given as yet, however it may prove of some importance in certain areas. Costa (11) confirmed Johnson's work and showed that while certain viruses (cucumber mosaic, cranberry false blossom) multiply in the dodder, others, such as tobacco mosaic and tomato aucuba mosaic do not. Nevertheless, they are transmitted by the dodder. Bennett (6) found that ability to transmit the virus varied with the species of dodder concerned. For example, mustard mosaic was transmitted by Cuscuta californica but not by the other two species used. The virus is apparently picked up by the haustoria from the phloem of the diseased plant and transferred to the phloem of the healthy plant by the same means.

Transmission of Leaf Roll

Leaf roll is one of the more readily transmissible viruses affecting the potato. In nature it is disseminated by means of infected tubers, possibly by the true seed, and is transmitted from diseased to healthy plants by aphids and perhaps other insects. Vine and tuber grafting are fairly efficient means of transmission.

From year to year the main source of infection is diseased tubers. Leaf-roll infected plants resulting from the planting of diseased sets supply the necessary inoculum for spread during the season. Generally the leaf-roll virus will render such stock valueless in three to four years, especially if no care is taken to rogue out diseased plants as soon as they appear.

The possibility of the virus being carried by the true seed of the potato was reported by Elze (21) in 1931. Further research along this line is required before the importance of this can be determined. Economically it will probably have little effect, as the potato is normally propagated by tuber sets rather than by seed.

Transmission of the virus from plant to plant in the field by aphids was first reported by Botjes (9). Schultz and Folsom (63) carried out experiments in 1921 which substantiate this claim. The aphids incriminated by these writers were Myzus persicae Sulz., and Macrosiphum solanifolii Ashm., and Aphis rumicis Linn. Since then other aphids have been found capable of carrying the disease. It is now known that Myzus pseudosolani Theob., M. circumflexus Buckt., and Aphis abbreviata Patch can also transmit the virus (22, 45). Of these six, M. persicae has proved to be by far the most efficient vector.

Considerable research has been carried out in an attempt to explain

the differences in the transmitting powers of these aphids. According to Smith (65), the feeding methods are practically identical. The stylet tract is, for the most part, inter-cellular, with the phloem strands the objective (see Fig. VII). Elze (22) considered that there is a definite biological relationship between M. persicae and the leaf-roll virus. He gives four reasons for his views:

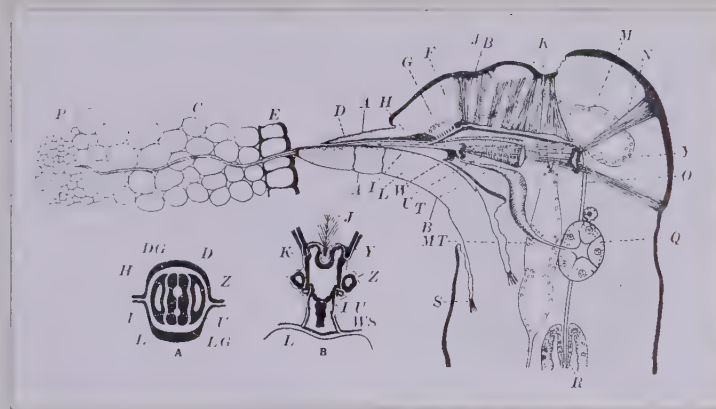
1. The existence of an incubation of the virus in the insect.
2. The retention of the infecting power of the insect after the moult.
3. The preservation of this power after the aphids have lived for about a week on plants not susceptible to leaf roll.
4. The great certainty with which a small number of individuals can transmit the disease. This was confirmed by Smith (66). The virus is not, however, passed on from the mother to her young.

Other insects, such as the tarnished plant bug, Lygus pratensis, (20), the capsid plant bug, Calcoris bipunctatus (45), and the leafhopper, Typhlocyba ulmi (44), and others, have been reported to transmit the virus of leaf roll. Reports, however, are conflicting.

Artificial transmission of leaf roll by means of grafting, either vine or tuber, is readily achieved. Schultz and Folsom (63) were among the first to report this method of dissemination. Scions from leaf-roll infected plants can be grafted onto healthy stalks. Shoots growing from the stalk below the graft develop leaf roll. Tuber grafting is accomplished by bringing the cut surfaces of a healthy tuber in contact with that of a diseased tuber. The two parts must be held together by some means. The methods of grafting employed in the experiments reported in this thesis will be described in detail later.

FIGURE VII

Schematic longitudinal section through the head of Aphis rumicis, showing the insect in the act of feeding. Davidson (13).



A, a section through the head in the plane AA; B, a section in the plane BB: C, cortex; D, labrum; DG, groove in labrum; E, epidermis; F, clypeus; G, gustatory organ; H, suction canal for plant sap; I, salivary canal; J, divaricator muscle of pharynx; K, pharynx; L, labium; LG, labial groove in which the stylets lie; M, brain; MT, thoracic ganglion; N, retractor muscles of the forehead; O, oesophagus; P, phloem; Q, salivary gland; R, valve to mid gut; S, retractor muscles of labium; T, salivary duct; U, left maxillary stylet; W, salivary pump chamber; WS, stem of salivary pump chamber; X, pump muscles; Y, tentorium; Z, left mandibular stylet.

Natural Spread in the Field

The distance and rate of spread of leaf roll in the field varies with the season and the locality. Generally the distance and spread from a given infected plant is quite limited. As already shown, the spread of leaf roll during the growing season is dependent on the aphid. Therefore, the abundance of these in any given district will largely determine the rate of dissemination. A further controlling factor is climate. This varies from season to season and naturally exerts a considerable influence on the activity of the plant lice as well as on the plant itself. Temperature, humidity, light, and wind all play their parts. It has been shown that, under favourable conditions, the insects may fly nearly a mile. The various effects of these factors on the leaf-roll plant and the insect vector are considered later. Diversity in these agencies explains the variation from year to year which is noted by various writers (30). The following table, taken from Murphy and Wortley (46) gives some indication of the distance of spread of leaf roll under field conditions in various parts of Canada.

Table 6. Spread of leaf roll from diseased to healthy plants in various parts of

Canada.

Location	Between 2 rows of leaf roll	Next row to leaf roll	Second row from leaf roll	Third row from leaf roll	Fourth row from leaf roll	Fifth row from leaf roll
Charlottetown, P.E.I.	15.0	21.2	2.5	2.5	0	0
Kentville, N.S.	35.0	12.5	6.5	1.2	2.5	1.2
Nappan, N.S.	20.0	16.2	0	0	0	0
Fredericton, N.B.	5.0	0	3.7	1.2	1.2	0
Lennoxville, Que.	17.5	17.5	0	0	0	3.7
Ottawa, Ont.	72.5	50.0	23.7	22.5	13.7	10.0
Thunder Bay, Ont.	0	0	0	0	0	0
Brandon, Man.	13.8	5.6	12.3	3.2	7.2	8.0
Indian Head, Sask.	5.3	1.4	1.4	0	0	0

Effect of Environment on Leaf Roll

The effect of environment on leaf roll of potatoes is so inter-related with its effect on the aphid vector that it is difficult to separate the two. As has been stated earlier, the spread of leaf roll is dependent on the abundance of its vectors. Therefore, any combination of climatic factors which will favour the development and dispersal of these insects will favour the spread of the leaf-roll virus. Nevertheless, the importance of the effect of climate on the host plant and the virus cannot be overlooked.

Under conditions of drought leaf roll spreads more rapidly than under normal conditions (77). There are a number of considerations here. In the first place, the host plants are developing slowly due to lack of food materials caused by the drought. In the second place, the aphid vector is very active under such conditions. The reason for this is lack of food supply. Plant juices are limited and are far more concentrated than when moisture supplies are good. This results in the production of winged migratory aphids as explained by Schaefer (61). These migrate readily to other plants in search of a more succulent host. Hence the spread of the virus, if present, is considerable.

Under conditions of high temperature and good moisture supply the spread of leaf roll is relatively small. The reasons here are somewhat the reverse of the above. With an abundant moisture supply plant juices are not concentrated and hence few, if any, winged migrants appear. There is another controlling factor here. Viruses have a rather low optimum temperature for development. The rate of multiplication of the viruses is greatly reduced if the temperature rises even one

or two degrees above this optimum.

Under shade conditions leaf roll spread is greatly reduced (78). The reason for this, as some writers suggest, may be due to the prevalence and rapid spread of a fungus disease of the vector during cloudy weather.

These points help to explain the seasonal variation in the prevalence and rate of spread of leaf roll in any given area.

Strains of Leaf Roll

Two strains or forms of leaf roll, which differ from true leaf roll, have been recognized. Quanjer (56) in 1923 describes a marginal type of leaf roll as follows: (see Heald (31) "The margins only of the leaflets are shortly curled upwards, often more in the upper part than in the lower portion of the plant. Leaflets do not take the upright habit. Transport of starch only prohibited in the margins. No phloem necrosis in midrib, petioles and stem." Holmes (34) lists marginal leaf roll as being synonymous with the virus of potato spindle-tuber.

Later, in 1929, Schultz and Bonde (62) described what they called apical leaf roll. It is similar to primary leaf roll in that rolling of the leaves occurs only in the upper portions of the plant. The lower leaves are never affected. Tubers of affected plants are generally small, but are normal in shape and number.

Varietal Resistance

Up to the present time no variety has been found which is immune to the leaf-roll virus. However, some do show a certain amount of resistance. Of the commercial varieties now grown in America, Katahdin

and Houma seem the most promising (74). During recent years a great deal of work has been done by crossing and seedling selection in an attempt to develop an immune variety. Thus far the workers in this field have met with failure. However, 18 seedlings which show high resistance have been developed (7). Probably in the not too distant future highly resistant or even immune varieties will appear on the market.

Host Range

Work which has been carried out to date seems to indicate that the host range of the leaf-roll virus is quite wide. Dykstra (19, 18) successfully transferred the disease by means of aphids from the potato to the following plants and back again: tomato, Lycopersicon esculentum; pepper, Piper sp.; Datura stramonium; D. tatula; Solanum nigrum; bitter nightshade, S. dulcamara; and nightshade, S. villosum. It can be seen that the danger of weeds serving as a reservoir for the virus is real. Insects can and do transmit leaf roll from infected weeds to the potato.

Insect Vectors of Leaf Roll

As was pointed out earlier, the definite vectors of leaf roll all belong to that group of insects commonly called plant lice or aphids. The family Aphidae is a very large one. Of its numerous members six appear to be responsible for the transmission of this disease in the field. These are:

Myzus persicae Sulz. - the green peach aphid.

M. pseudosolani Theob. - the foxglove aphid.

M. circumflexus Buckt. - the lily aphid.

Macrosiphum solanifolii Ashm. - the pink and green potato aphid.

Aphis abbreviata Patch - the buckthorn aphid.

A. rumicis Linn. - the bean aphid.

Of these the former, M. persicae, is by far the most important, not only because it is extremely efficient as a vector of the leaf-roll virus, but also because it is most universally distributed.

As regards the transmission of leaf roll by insects other than aphids, only conflicting evidence is available. Elze (20) reports transmission by Lygus pratensis, Psylliodes affinis and Eupteryx auratus. Of these the last two are not found in the Edmonton district. L. pratensis, although present, is not very common. However, a closely related species, L. elisus, is abundant here. All of the tarnished plant bugs taken in 1944 were of this latter species. It feeds on a very wide range of plants, including the potato. Murphy (44) showed that Calcoris bipunctatus and Typhlocyba ulmi were also vectors of the disease. However, Smith (67,68) was unable to obtain transmission by any of the latter four named insects. His experiments did not, however, include L. pratensis.

In view of this evidence it is not considered that these require any further consideration at this time. The following material will be more or less confined to the aphids already mentioned above.

Myzus persicae Sulzer

Distribution This aphid is probably the most widespread of all the Aphidae. There are, in fact, probably few parts of the world where it is not present. Smith (70) reports it as being common Europe, North

and South America, North and South Africa, Australia, New Zealand, Japan, India, Iraq, and Bermuda. Myzus persicae has been found in the Edmonton district.

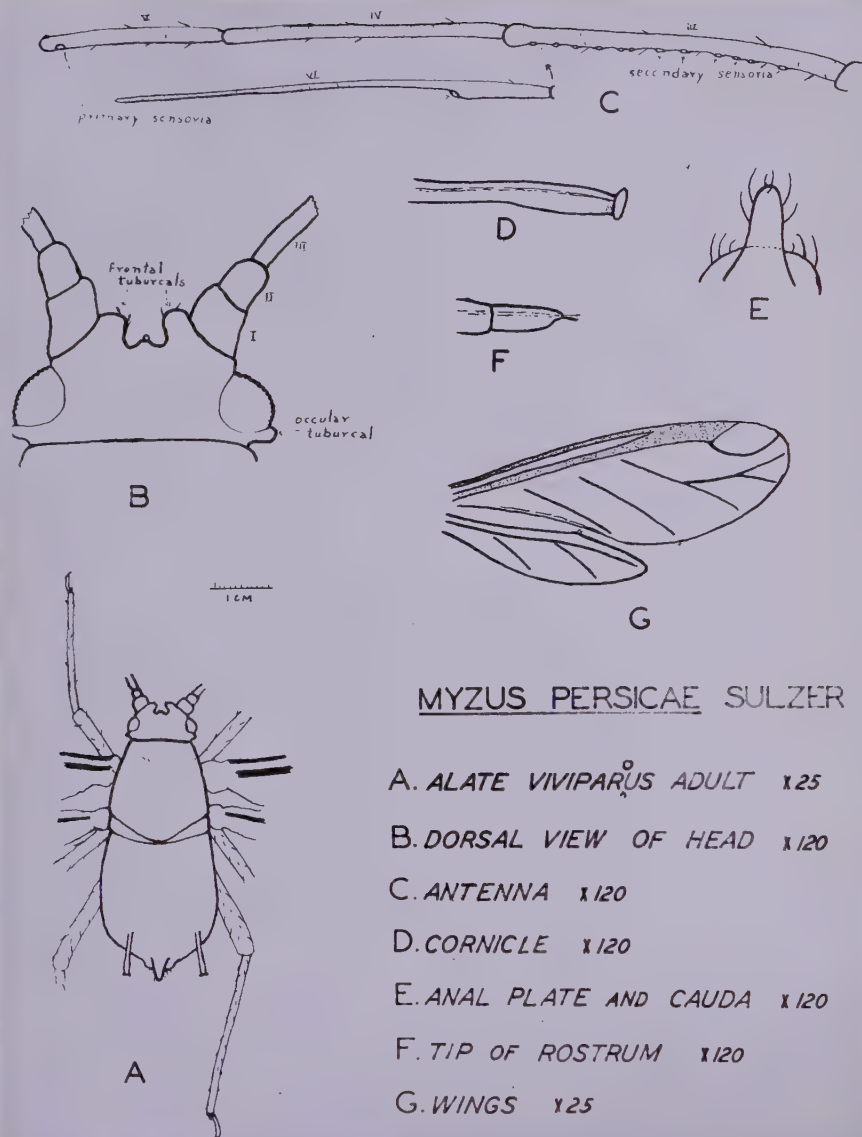
Description For a complete description of the various forms of M. persicae Sulz. the reader is referred to Theobald's "British Aphides". Theobald's description of this species can be found in Smith (70), page 538. The reader is also referred to Gillette (27), page 359. See Figure VIII.

Food Plants This species is one of the most omnivorous of the Aphidae. Samuel (58) reports it as feeding on 21 host plants of Cruciferae, Malvaceae, Leguminosae, Rosaceae, Compositae, Orobanchaceae and Solonaceae. Smith (70) states that some of its most important food plants in Europe are: Brassica oleracea, Brassica spp., Beta vulgaris, Solanum tuberosum, Nicotiana spp., and other solanaceous plants; peach, nectarine, plum, cherry, almond, Euonymus spp., and tulips. Taylor (75) in west Colorado found these aphids on peach, nectarine, plum, prune, cherry, choke-cherry, sand-cherry, turnip, rape, cabbage, tomato, potato, false-mallow, yellow-dock, redroot, mustard, shepherd's purse, rhubarb, snapdragon, carnation, egg-plant, and, more rarely, on pear, apple, crabapple, willow and cultivated rose. Patch (53) lists 313 host plants in 68 families.

Life History In spite of the fact that this aphid was described and named by Sulzer as early as 1761, little was known of its life history until fairly recent times. In part, this may have been due to the variation in the form of the spring and fall migrants. According to Taylor (75) the eggs are laid in the fall on peach, plum and cherry.

FIGURE VIII

Drawings of the aphid Myzus persicae Sulzer



Here at Edmonton the winter host is the rose. The eggs are placed singly under the buds or rough bark near the tip of the young twigs. In western Colorado the eggs hatch early in April, the actual time varying with the temperature. The young are dark green at first, but gradually become lighter in colour. As the buds open the stem mothers take on a pinkish colouration, although all degrees of shading between green and salmon pink are known. Late in the spring, during the latter part of May and early June, winged migrants appear and travel to their summer hosts. Here the aphids thrive throughout the summer. Early in the fall winged migrants are again produced. These return to the winter hosts. Sexual forms develop, mate, and lay eggs. These eggs are green at first but soon become black.

Myzus pseudosolani Theob.

Distribution These aphids are fairly widely distributed throughout Europe, Great Britain and America.

Description For a detailed description of the various forms refer to Theobald as reported by Smith (70), page 542, and Gillette and Palmer (29), page 206.

Life History These aphids lay their eggs on the foxglove in the early fall. The eggs hatch in the spring into wingless stem mothers. These hide in the folded leaves and they usually escape notice. They generally require a month to reach maturity. The third generation develops wings and flies to summer hosts. As noted below, the host range of the foxglove aphid is very great. Late in the summer fall migrants return to the foxglove, where wingless males and oviporous females develop. These mate and eggs are laid. Patch (52).

Food Plants These aphids have a wide host range. Patch (53) lists 71 hosts belonging to 31 families.

Myzus circumflexus Buckt.

Distribution These aphids are widely distributed in Great Britain, Europe, and North America.

Description For detailed descriptions of these aphids the reader is referred to Smith (70), page 537, and to Gillette and Palmer (29), page 202.

Life History The author was unable to obtain literature dealing with the life history of this aphid. However, it is said to be a common pest of greenhouses and may escape from them during the summer months. There is no evidence that this species is present in Alberta.

Food Plants Like the other aphids already considered the host range of this species is quite large. Patch (53) lists 80 host plants belonging to 35 families.

Macrosiphum solanifolii Ashm.

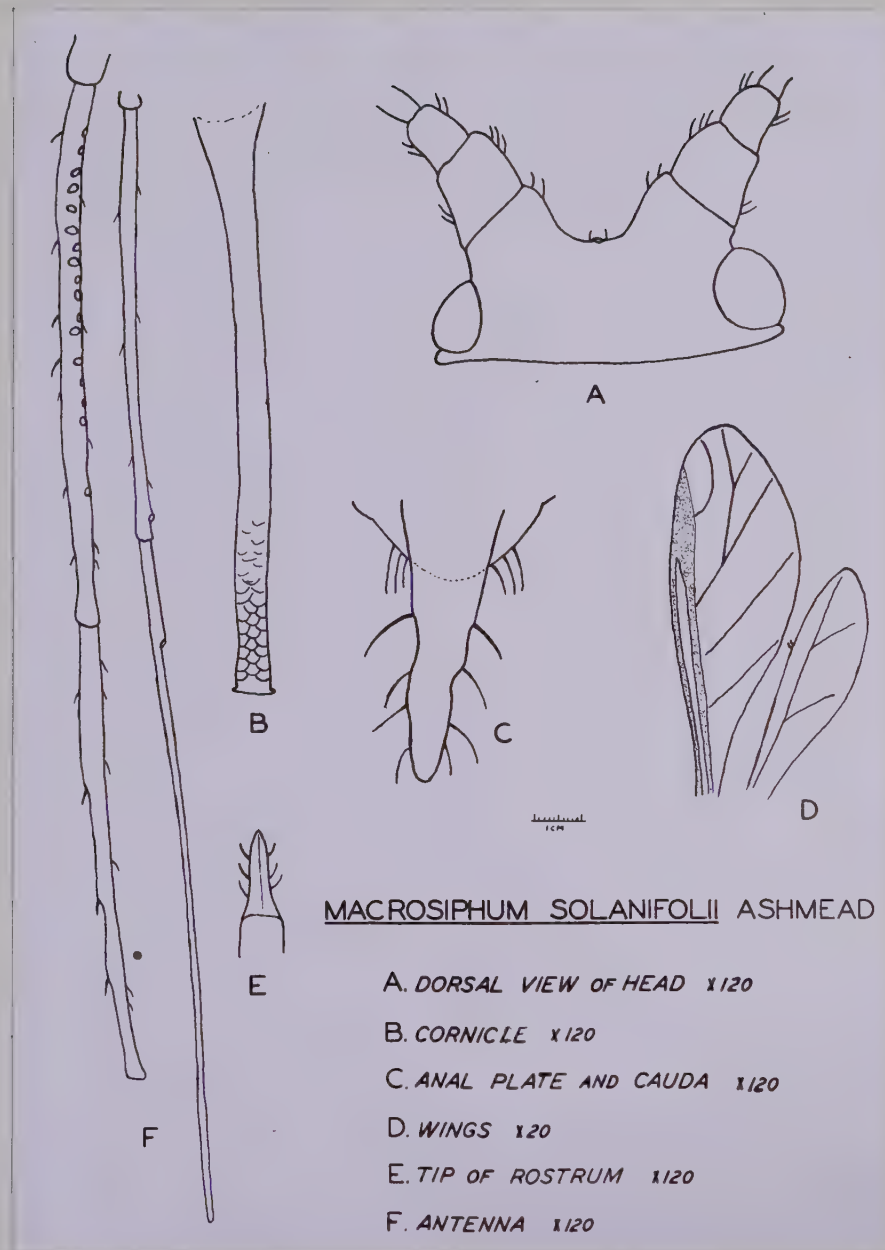
Distribution These aphids are widely distributed throughout Europe, the British Isles, Canada, the United States, and Egypt. This aphid is very common in Edmonton and district.

Description For detailed descriptions of the various forms of M. solanifolii consult Smith (70), page 532, Patch (49), page 208, and Gillette and Palmer (29), page 195.

Life History These aphids overwinter in the egg stage on the rose.

FIGURE IX

Drawings of the aphid Macrosiphum solanifolii Ashmead



Stem mothers hatch out in May and when mature begin to produce both winged and wingless offspring. The main migration from the rose to the summer host, the potato, occurs early in July. On the potato the aphids develop rapidly. Early in the fall winged migrants again appear, which return to the rose. Sexual forms are produced and the eggs are laid.

Food Plants These aphids have an even wider host range than the two preceding species. According to Patch (53) they will feed upon 115 plants belonging to 35 different families.

Aphis abbreviata Patch

Distribution These aphids apparently are widespread in Great Britain, Europe, and America. This species is known to be present in the Edmonton district.

• Description For description of this species refer to Smith (70), page 521, Patch (51), page 43, and Gillette and Palmer (28), page 379.

Life History The winter is passed in the egg stage on the buckthorn. These hatch in the spring into wingless stem mothers. When mature these reproduce parthenogenically. The winged individuals migrate to various summer food-plants, where they build up colonies. Early in the fall winged migrants (~~sexualae~~) return to the buckthorn, where they produce wingless oviparous females. At this time winged males, developed on the secondary host, return to the buckthorn and mate with the females. Eggs are then laid under the leaf buds.

Food Plants The host range of A. abbreviata is somewhat less than the foregoing. Patch (53) lists 67 food plants belonging to 29 families.

Aphis rumicis Linn.

Distribution A. rumicis is widely distributed throughout Europe, Great Britain, Africa, India, Formosa, Japan, North America, Brazil, Sakhalin.

Description The reader is referred to descriptions by Smith (70), page 524, Davidson (14), page 81, and Gillette and Palmer (28).

Life History In Europe the winter host is generally the spindle tree or dock; in America the pigweed serves this purpose. Other plants, however, may also serve as the primary host. The eggs hatch in the spring and in due course winged viviparae develop which migrate to various secondary food plants. These serve throughout the summer. In the fall migrants return to the winter hosts, where they give birth to wingless oviparae. These mate with winged males which develop on the secondary host at this time. Eggs are laid in an irregular manner on the stems about the buds. Although these are yellow when laid they soon turn black.

Food Plants The host range is considerable. Patch (53) names 196 food plants in 49 separate families.

Effect of Environment on the Aphids

As has already been stated, any combination of factors/^{which} will further the development and dissemination of the aphid vectors will increase the spread of leaf roll. There are various environmental factors to be considered here, the most important being temperature, humidity, and wind. As will be at once realized, these are very closely interdependent.

Considerable information is available regarding the effects of temperature and humidity on rate of development and reproduction.

Reports are all to the effect that the rate of development increases as temperature and humidity approach the optimum for the species (5, 13, 12). As reported by these authors, there exists a similar relationship between temperature and humidity and reproduction. In all cases the effect of humidity is greatest when the temperature is favourable. Temperature, however, generally exerts the greatest controlling power.

The effect of light does not appear to be as important. However, shading does reduce infestation (13). Whether this is due directly to the lack of light or to the rapid spread of disease under such conditions has been suggested before, but has not been definitely determined.

The effect of wind does not concern development and reproduction to any extent. However, parts of plants generally exposed to high winds will not be heavily infested at any time. The main influence of wind is on flight. Davies (16) and others have determined that aphids will not take flight of their own accord if the wind velocity is above three or four miles per hour. Gales of 70 miles per hour or more will not dislodge many of them from the leaf or stem on which they feed. Generally speaking, migration is encouraged by high temperature, low relative humidity, and low wind velocity (15, 17). Under favourable conditions, aphids will fly up to half a mile or more from their point of dispersal. (Patch, 50).

THE PROBLEM

As stated in the beginning the primary object of this investigation was to determine what insect vectors of the leaf-roll virus are present in the Edmonton district. Information regarding their relative abundance was sought. Data were collected by conducting a survey of potato fields about Edmonton. Insects were collected, counted, and identified.

A further object of this investigation was to determine if tuber phloem necrosis, as associated with leaf roll is the result of:

- (a) The leaf-roll virus alone;
- (b) A toxin secreted by the insect vector, Myzus persicae; or
- (c) The virus plus a toxin secreted by the vector.

Data on this problem were secured by field and greenhouse experiments in which the virus was transmitted to healthy potato plants by, (a) grafting, (b) non-viruliferous insect cultures, and (c) viruliferous insect cultures.

EXPERIMENTAL METHODS AND RESULTS

Data were collected from field surveys and controlled experiments. The survey of potato fields in the Edmonton area supplied information on the occurrence and abundance of the various insects found in association with potato plants as well as other information pertaining to the problem. Transmission experiments were conducted and the data obtained are reported under the following headings: (a) Insect transmission; (b) Tuber grafting; and (c) Vine grafting experiments.

Survey of Five Potato Fields Near Edmonton

In order to determine the different species of aphids present on potatoes at Edmonton, and their relative abundance, a survey was made for this purpose during the summer of 1944. Five fields near Edmonton were chosen for this purpose. In the selection of these fields various factors were considered, namely, their size, condition, uniformity, and the stage of development of the crop, and its variety. A reasonable uniformity in regard to these points was necessary in order to get comparable results.

The average size of the fields selected was three acres. Such fields were large enough to ensure a reasonably normal distribution of the aphid population. Furthermore, the fields were of such a size that counts could be taken away from the edge of the plots where the direct influence of adjoining vegetation might be considerable. Also, such fields contained a large number of plants, so that an accurate estimation could be made of the percentage of leaf roll present. At the time of selection only a trace of the disease was evident in these fields.

In each of the fields the crop was well cultivated and fairly free from weeds throughout the season. The potato plants were about eight to ten inches in height on July 12, 1944, when the fields were chosen.

The fields selected had been planted to potatoes of the Netted Gem variety. The reason for keeping to the one variety is evident from what has been said earlier, namely, differences in varietal susceptibility. Although no variety is immune, the effect of the virus varies considerably in different varieties. Also, there is a possibility that the vector may have a preference for certain varieties, in which case some of these would be attacked more severely than others.

Two methods of securing an estimate of the aphid population were compared. One consisted of picking 100 leaflets at random from the field, and the other method was to take the complete compound leaves. Both methods were tested out on the same day in the same three fields. Samples were taken in triplicate. Results indicated no significant difference in counts. The first mentioned method was chosen because it entailed handling less material. The actual survey began on July 14, 1944. The leaflets were selected at random throughout the plot. Each leaf, as picked, was dropped into a paper bag, which, when the 100 leaves had been obtained, was securely closed by means of paper clips. On returning to the laboratory these bags were placed immediately in the refrigerator until a count could be made. The results of these counts, made at approximately ten-day intervals, are shown in Table 7.

Table 7. Number of aphids per 100 leaflets.

Date	Aphids per 100 leaflets					Average
	Field #1	Field #2	Field #3	Field #4	Field #5	
July 14	2	11	3	16	7	7.8
July 22	11	17	10	15	12	13.0
Aug. 2	14	46	20	34	17	26.2
Aug. 14	10	29	9	15	6	13.8
Aug. 25	3	12	9	16	9	9.8
Sept. 5	5	5	13	18	9	10.0
Average	7.5	20.0	10.7	19.0	10.0	

The data in Table 7 show a more or less gradual increase in the aphid population up to August 2, which is the peak in all cases. However, the period of heavy infestation seems to extend about four weeks, from July 22 to August 14. After August 2 there was a gradual decline in the number of aphids present. This may have been due in part to the decreasing rate of reproduction and development resulting from gradually lowering fall temperatures. It may also indicate that at this time the aphids were beginning to return to their winter hosts. It is not the ordinary general summer migrant, but another form, the sexualae, which returns to the winter host plant. These sexualae are practically identical with the summer viviparous alates. In some species they are somewhat larger.

Another point which is evident here is that fields Nos. 2 and 4 had apparently become infested somewhat earlier than the others, and, throughout the season, maintained a greater aphid population. Table 10 shows that these are the only fields which had the wild rose growing

in the immediate vicinity. The significance of this is not definite. It is known that the rose is the main overwintering host of Myzus persicae and Macrosiphum solanifolii, but the indication is that the cultivated rose is preferred to the wild species. If further observation reveals that the wild rose is a major winter host, an explanation for the early infestation of these fields has been found. It is only natural that those fields closest to the centres of dispersal would be infested earliest and heaviest.

Identification of Aphids Collected during Field Survey

The aphids collected during the survey were identified by the writer. All species were carefully checked with detailed descriptions. Specimens, known definitely to be Myzus persicae, were available for comparison. However, as yet it has been impossible to get the material checked by a specialist. The data in Table 8 indicate the relative abundance of the various species taken, and refer to wingless forms unless otherwise indicated. Those appearing in the column "Unknown" are all wingless forms of apparently the same species. However, no winged individuals comparable to these were taken, hence identification could not be made. As nearly as can be determined, however, they have not been recorded as vectors of leaf roll. That is, they do not check with the description of wingless forms of any of the six known leaf-roll vectors.

Those appearing in the column "Others" are probably only accidental visitors on the potato plant. Their main host plant is not the potato. Hylopterus atriplicis feeds normally on lamb's quarter; Macrosiphum granarium on various grains and grasses; and Macrosiphum dirhodum on grains, grasses and the rose. All these plants were growing near the

potato fields surveyed.

Myzus persicae and Macrosiphum solanifolii were the only leaf-roll carriers found on potatoes in the Edmonton district in 1944. The latter was by far the most abundant.

According to Table 7 the aphid population was high in fields Nos. 2 and 4, and relatively lower in the other three. Table 11 indicates that the estimated percentages of leaf roll present in the fields were greatest in fields Nos. 2 and 3, and low in the others. There is, therefore, no correlation between aphid population and the percentage of leaf roll evident. However, in Table 8 it will be seen that M. persicae, which is by far the most efficient vector of leaf roll, was most abundant in those fields having the highest percentage of leaf-roll infection. Whether this evidence is significant or not remains open to question. In the first place, there is generally a time lag in the appearance of leaf-roll symptoms. That is, it is some time after infection occurs before symptoms are evident. In fact, most of the leaf roll seen in a given season traces to infection in the previous year. In other words, the higher incidence of disease in fields Nos. 2 and 3 may have been mainly due to the percentage of leaf roll in the "seed" material. In the second place, various factors of climate and other agencies combine to make a definite determination of leaf roll by plant symptoms difficult or impossible the same year as infection takes place. It would, therefore, require more extensive tests and more than one year's results before a definite statement could be made on a correlation of this sort.

It should be noted here that in 1936 aphids identified as Aphis abbreviata Patch were collected in the Edmonton district by Professor Strickland. However, this species was not collected in the potato fields surveyed in 1944.

Table 8. The relative abundance of the various aphid species found on potato plants at Edmonton in 1944.

Field Number	Date	<u>Myzus persicae</u>	<u>Macrosiphum solanifolii</u>	Others	Unknown	Total
1	July 14		2			2
	July 22	2	3		5	11
	Aug. 2		8		6	14
	Aug. 14		7		3	10
	Aug. 25		3			3
	Sept. 5	3	2		5	5
2	July 14	5	6			11
	July 22	5	7, 1 winged	5 <u>Hylopterus atriplicis</u>		17
	Aug. 2	10	24	7 <u>H. atriplicis</u>	5	46
	Aug. 14	5	20		4	29
	Aug. 25		7		4	11
	Sept. 5		3		2	5
3	July 14		3			3
	July 22		5		5	10
	Aug. 2	5	12		3	20
	Aug. 14	3	6			9
	Aug. 25	2	7			9
	Sept. 5	6	5		2	13
4	July 14		9		7	16
	July 22		8		7	15
	Aug. 2		27	1 <u>Macrosiphum dirhodum</u>	6	34
	Aug. 14	4	5		6	15
	Aug. 25		9	1 <u>Hylopterus atriplicis</u>	5	16
	Sept. 5	1	11, 1 winged		6	18
5	July 14		3		4	7
	July 22		8	1 <u>H. atriplicis</u> , winged	3	12
	Aug. 2		5	7 <u>H. atriplicis</u>	5	17
	Aug. 14	1	5			6
	Aug. 25	1 winged	6		2	9
	Sept. 5		6	1 <u>Macrosiphum granarium</u> , winged	2	9

Field Sweeps

On the same day that the aphid counts were taken sweeps were made in the fields surveyed. The insects collected were killed and determinations made. The reason for making these sweeps was to determine whether or not any of those insects, other than aphids, which have been reported as leaf-roll vectors, were present in these fields, and, if so, in what numbers. The various insects and figures representing their relative abundance are given in Table 9.

A glance at Table 9 is sufficient to indicate the very wide variety of insects which may be associated with the potato plant. The vast majority of these have never been considered leaf-roll vectors. The aphids included here are those collected in the sweeps. They are included to indicate their relative abundance in relation to the other insects present. The figures given in this table are only approximate. The Cicadellidae have been associated with the transmission of numerous viruses, but their numbers and irregular appearance eliminates them as leaf-roll vectors of any importance in the Edmonton district. This leaves the Miridae as the only group that needs any great consideration. Of the Miridae collected by far the largest percentage proved to be the western tarnished plant bug (Lygus elisus).

Lygus pratensis is the only tarnished plant bug which has been reported to be a leaf-roll vector. This report, as has been previously stated, is refuted by other workers. It is therefore impossible to say without extensive tests whether or not these insects are important leaf-roll vectors. That the tarnished plant bugs do carry certain virus diseases is known. Nevertheless, their importance with regard to leaf-roll transmission must be regarded as questionable, at present.

Table 9. Insects collected in field sweeps.

Order	Insect Family	Number of insects collected																								
		I ^a					II					III					IV					V				
		1 ^b	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Coleoptera	Coccinellidae									1					1											1
Diptera	Agromyzidae									13	6															
	Anthomyidae	2			1		1	2				2	1				2	1				1		2	1	
	Bibionidae								1															1		
	Calliphoridae		3			1						2					1									
	Cecidiomyidae						27	5															4			
	Chironomidae	1	2	1	5		2		2	4		1		2	6		1			6			1	1	1	
	Chloropidae	1	15	20	27			20	24	46	7		16	30	51	25		16	30	45	86		6	17	40	15
	Culicidae						4		1																	
	Dolichopodidae				2			1	5	1	2			1	2											
	Lauxaniidae			4	5				1	2				1	3	2		1		12	1			8	1	1
	Simulidae						1			1																
	Syrphidae						1					1											2			
	Tipulidae			1		3	1		2	2		1					1		3	1						
	Others					1	13			8	1				3	2				2	2					4
Hemiptera	Anthocoridae				1																					
	Lygeaidae				1																					
	Miridae	3	6	5		12	6	5	8	19	14	8	4	7	9	15	4	2	4	9	11	2	5		6	11
Homoptera	Aphidae	2	10	35	5	5	2	25	80	30	13	3	13	31	7	18	6	9	37	12	13	4	10	24	7	20
	Cicadellidae				5	2									3	6		2		3	2					3
	Membracidae																		2							
	Psyllidae									2										1				1		
Hymenoptera	Chalcicoidea						1																			
	Ichneumonidae				2					1										2						3
	Others							1								1		2								
Thysanoptera							1																			

a. Field number.

b. 1, July 14; 2, July 22; 3, August 2; 4, August 14, 5, August 25.

Surrounding Vegetation

A record was kept of the vegetation present in the area immediately surrounding the fields selected for the survey. The purpose of this was to determine if any plants existed there which might have acted as winter or even early spring hosts for the aphids present on the potatoes during the summer.

From Table 10 it can be seen that the only plants common to all fields were the dandelion, lamb's quarter, red root pigweed, poplar and willow. According to Patch (53), the first three are hosts of Myzus persicae. Lamb's quarter and red root pigweed are hosts to all the leaf-roll aphid vectors considered, with the exception of M. circumflexus. Although the common poplar does not seem to be a host of any of the leaf-roll vectors, M. persicae will feed on the willow. None of these plants serve as winter hosts for any of the known leaf-roll vectors.

As already pointed out, the wild rose was found adjacent to both those fields which supported the largest aphid populations. Whether this indicates that the wild rose is an important winter host of M. persicae and Macrosiphum solanifolii is doubtful. The cultivated rose is preferred to the wild species by both these aphids. No survey was made to determine the location of cultivated roses in relation to the potato fields examined. An extensive investigation should be made to determine the importance of the wild rose as a winter host of these aphids.

It should be noted here that this survey was not extensive enough to eliminate all possibilities. As reported by Patch (50), the migrating aphids will travel up to one-half mile or more. Infestation may, therefore, come from vegetation some distance removed from the field.

The first of these is the fact that the
information is being released to the public.
The second is the fact that the information
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which is not only accurate but also
comprehensive.

The third is the fact that the information
is being released to the public in a form
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public in a form which is not only
accurate but also comprehensive.

Table 10. Plants found in the immediate vicinity of the potato survey fields.

Botanical name	Common name	Field number				
		1	2	3	4	5
<u>Agropyron tenerum</u>	Rye grass	1			1	1
<u>Amaranthus retroflexus</u>	Red root pigweed	1	1	1	1	1
<u>Avena sativa</u>	Oats					1
<u>Axyris amarantoides</u>	Russian pigweed			1	1	1
<u>Brassica arvensis</u>	Wild mustard					1
<u>Bromus inermis</u>	Brome grass					1
<u>Capsella bursa-pastoris</u>	Shepherd's purse			1		
<u>Caragana arborescens</u>	Caragana			1		
<u>Chenopodium album</u>	Lamb's quarter	1	1	1	1	1
<u>Coringia orientalis</u>	Hare's ear mustard	1				
<u>Hierochloe odorata</u>	Sweet grass		1		1	
<u>Hordeum jubatum</u>	Wild barley			1	1	1
<u>Hordeum sativum</u>	Barley		1			
<u>Melilotus alba</u>	Sweet clover	1				
<u>Mentha spp.</u>	Mint	1				
<u>Neslia paniculata</u>	Ball mustard				1	
<u>Phleum pratense</u>	Timothy				1	
<u>Picea canadensis</u>	Spruce					1
<u>Polygonum convolvulus</u>	Wild buckwheat	1			1	
<u>Polygonum Tartaricum</u>	Tartarian buckwheat	1				
<u>Populus spp.</u>	Poplar	1	1	1	1	1
<u>Rosa spp.</u>	Rose		1		1	
<u>Ruba spp.</u>	Raspberry		1			1
<u>Salix spp.</u>	Willow	1	1	1	1	1
<u>Sisymbrium incisum</u>	Tansy mustard				1	
<u>Spergula arvensis</u>	Corn spurey	1				
<u>Taraxacum spp.</u>	Dandelion	1	1	1	1	1
<u>Trifolium hybridum</u>	Alsike clover		1	1		
<u>Trifolium repens</u>	White Dutch Clover	1				

Percentage Leafroll Present in the Fall

To determine the percentage of leaf roll present in the survey fields, five groups of 100 plants were examined in each. The count was made on September 5, 1944. The plants were examined consecutively as they appeared in the rows. One hundred plants in each of five different rows were inspected. In cases where, due to mechanical injuries or the presence of other diseases, a definite determination could not be made, the plant in question was omitted from the count. The results

are given in Table 11.

Table 11. Estimated percentage of leaf roll present in the potato fields surveyed.

Count of 100 plants	Percentage of leaf-roll plants				
	Field 1	Field 2	Field 3	Field 4	Field 5
First	7	3	7	4	7
Second	3	8	10	6	2
Third	3	7	8	2	3
Fourth	5	8	6	2	4
Fifth	1	3	7	4	2
Total	19	39	38	18	18
Average (%)	3.8	7.8	7.6	3.6	3.6

Weather Records

The writer wishes to thank the University Department of Field Crops for the weather records reported in Table 12. In Table 13 the information given in Table 12 is broken down into three periods. The period of heaviest aphid infestation, July 18 to August 17, is compared with periods of equal length preceding and following. Precipitation decreased progressively throughout the summer and apparently had little effect on the aphid population. Temperature may have had some influential effect, however. The temperature during the second period was, on the average, three degrees or more above that in either of the other periods. This is sufficient to have had a considerable effect on the rate of reproduction as well as on the rate of development.

Breaking this down still more, as in Table 14, into the periods

Table 12. Daily weather records for June, July, August and September, 1944.

Day	J u n e				J u l y				A u g u s t				S e p t e m b e r ^a			
	Aphis	Sun-	Precip-	Temper-	Aphis	Sun-	Precip-	Temper-	Aphis	Sun-	Precip-	Temper-	Aphis	Precip-	Temper-	
	count	shine	itation	ature	count	shine	itation	ature	count	shine	itation	ature	count	itation	ature	
		hr.	ins.	Max. Min.		hr.	ins.	Max. Min.		hr.	ins.	Max. Min.		ins.	Max. Min.	
1		7.0	0.40	70 51		2.3	0.03	63 50		13.8	-	72 44		-	64 49	
2		0.2	0.05	58 53		5.3	0.05	63 50	26.2	12.7	0.08	79 47		-	72 40	
3		0.0	0.16	52 45		15.3	-	72 42		9.3	0.01	79 52		0.03	75 37	
4		4.5	-	56 40		14.0	0.05	81 47		11.8	-	81 54		-	65 47	
5		14.1	-	65 39		9.7	0.38	76 50		11.1	0.03	80 52	10.0	-	75 38	
6		14.3	-	71 40		0.0	0.43	52 50		11.0	-	74 49		tr.	82 39	
7		13.5	-	75 43		11.3	0.10	63 43		4.1	tr.	68 52		-	73 47	
8		14.8	-	79 49		1.4	0.40	61 47		13.8	-	76 43		tr.	75 45	
9		14.5	-	81 45		11.6	-	68 44		9.7	0.02	78 48		-	76 41	
10		15.1	-	81 49		9.6	0.02	74 46		5.0	tr.	63 52		-	85 43	
11		13.5	0.15	80 55		10.2	-	73 50		2.1	0.08	72 43		-	84 42	
12		0.0	0.42	58 51		2.4	tr.	73 52		8.7	0.04	66 47		-	85 44	
13		0.0	1.75	56 50		9.8	0.38	68 46		6.7	tr.	64 46		tr.	82 49	
14		0.0	1.31	53 50	7.8	10.0	-	72 51	13.8	9.8	tr.	69 39		0.01	59 50	
15		0.0	0.42	52 48		11.8	0.15	74 51		8.0	tr.	68 44		0.02	56 43	
16		0.0	0.12	53 47		13.2	0.07	72 49		9.3	-	70 37		0.41	53 38	
17		1.2	-	56 45		14.8	-	73 49		8.2	0.03	76 42		0.03	46 38	
18		13.6	-	63 38		15.1	-	79 49		3.3	tr.	62 51		0.03	50 38	
19		10.3	tr.	74 45		15.1	-	81 52		6.0	0.01	67 45		0.06	48 32	
20		4.5	tr.	59 47		12.9	tr.	80 55		11.1	tr.	71 44		tr.	50 35	
21		10.8	-	71 46		8.9	-	76 57		8.9	tr.	67 47		-	53 42	
22		10.5	0.03	70 46	13.0	13.7	-	80 54		9.7	-	70 42		tr.	68 44	
23		8.4	0.01	70 49		9.5	0.16	87 55		13.2	-	77 43		tr.	70 43	
24		3.5	tr.	67 51		4.8	0.01	73 61		6.4	0.03	74 47		0.39	56 44	
25		10.9	tr.	65 47		7.3	tr.	71 50	9.8	5.2	0.05	73 50		0.03	58 47	
26		10.5	tr.	69 46		14.5	-	79 48		7.5	tr.	72 42		-	61 42	
27		14.4	0.03	73 42		12.5	0.32	80 53		11.2	0.18	73 46		-	62 32	
28		10.7	-	81 50		7.9	0.12	75 57		1.5	0.16	63 53		0.14 ^b	55 34	
29		14.8	-	83 51		0.0	0.21	65 55		7.8	tr.	69 44		0.04 ^b	33 29	
30		6.8	0.20	84 53		0.0	0.21	60 49		12.8	-	76 40		-	37 18	
31						0.7	0.17	60 51		11.6	-	83 44				
Total		242.4	5.05			275.6	3.26			271.0	0.72			1.18		
Mean				67.5 47.0				71.7 50.4				72.0 46.1			63.6 40.4	

a. Sunshine data not available.

b. Rain and snow.

between aphid counts, it is found that the mean temperature was highest for the period July 15 to 22. The mean temperature decreased gradually from this time on, but remained fairly high until after the end of July. The aphid population was greatest on August 2. It will appear, therefore, that there is a lag between the temperature effect and the greatest aphid population. However, this probably is only apparent. The warm period in mid-July would result in rapid reproduction and growth. There would thus be built up a large population of mature or nearly mature individuals. This large population, reproducing at a slower rate because of decreasing temperatures, could produce sufficient numbers to increase the total population for a time. The almost total lack of rainfall during August may have been partly responsible for the fairly constant aphid population during the latter part of this month.

Table 13. Average conditions during the periods indicated.

Period (inclusive)	Hours sunlight	Precipitation in inches	Temperature, °F.		
			Av. daily max.	Av. daily min.	Av. mean temp.
June 18 to July 17	282.4	2.33	69.8	47.6	58.7
July 18 to Aug. 17	277.7	1.49	73.5	49.6	61.6
Aug. 18 to Sept. 17	not available	.93	70.1	44.1	57.1

Table 14. Average daily records for the periods between aphid counts.

Date	Hours sunlight	Precipitation in inches	Aphid count at end of period	Temperature, °F.		
				Av. Max.	Av. Min..	Mean
July 4 to 14	8.0	0.25	7.8	68.9	47.5	58.5
July 15 to 22	12.7	0.11	13.0	75.9	51.6	64.4
July 23 to Aug. 2	7.7	0.17	26.2	72.9	52.4	62.3
Aug. 3 to 14	8.8	0.04	13.8	73.3	48.8	60.3
Aug. 15 to 25	8.5	0.02	9.8	70.1	42.7	57.6
Aug. 26 to Sept. 5	--- ^a	0.23	10.0	71.4	44.7	57.5

a. Not available.

Field Experiments in Leaf-Roll Transmission

Insect Transmission Experiments

At present the development of necrosis of the phloem elements in potato tubers is believed to be due to the primary incidence of the leaf-roll virus in the sap of healthy plants. Apparently no one has yet attempted to show whether this necrosis will develop when the insect vector does not carry the virus or when the virus is transmitted by grafting methods. (Confirmed by Dr. Donald Folsom, Orono, Maine, in correspondence with Dr. G. B. Sanford.) The case of the sudden development of necrosis of the phloem elements in potato tubers as associated with the feeding of the tomato psyllid on potato vines, and the apparent absence of a virus, has already been cited (60). In view of this evidence an experiment was planned to show whether aphids, free from the leaf-roll virus can initiate necrosis of the phloem. Preliminary work on this general problem was begun by the Dominion

Laboratory of Plant Pathology in 1941, but a study of the part played by aphids was not included until 1944.

On June 17, 1944, about 120 sets of Carter's Early Favorite were planted in the field. This was foundation stock produced under rigid field inspection and later tuber indexed and found free from leaf roll.

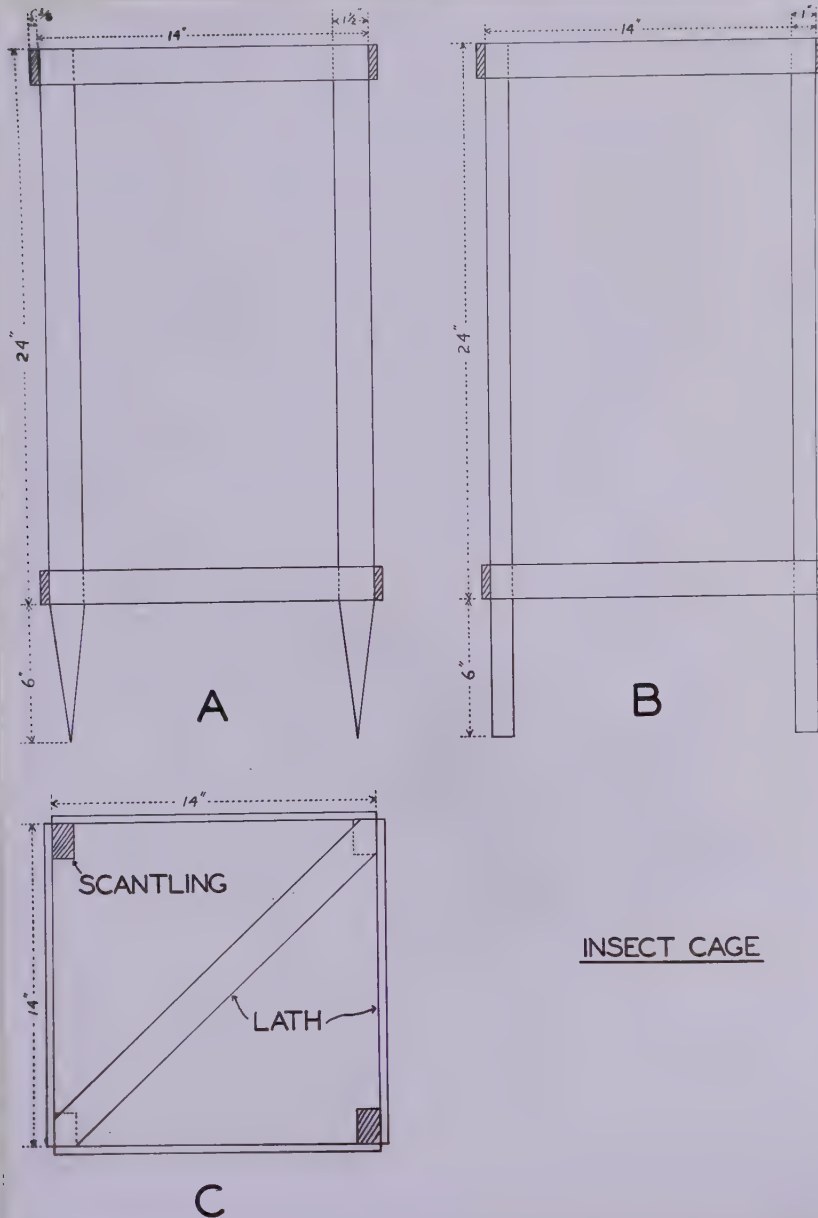
A total of 25 plants were used in each replicate of the experiment. Seven of these plants were infested with a non-viruliferous population of aphids, 13 with a viruliferous population, and 5 were uninfested controls. The plants infested with aphids were covered with insect cages (Figure X), but the controls were not. The experiment was repeated three times during the season, namely, July 11, July 26, and August 11.

The vector, Myzus persicae, obtained through the courtesy of Mr. D. J. MacLeod, Dominion Laboratory of Plant Pathology, Fredericton, N.B., was used in these transmission experiments. The non-viruliferous population of aphids was raised on the leaves of turnips, and the viruliferous population was raised on leaf-roll infected potato vines. The aphids were removed from their host by means of a fine camel-hair brush and transferred to the potato plants in the field. The aphids were allowed to remain on these plants for approximately two weeks. To kill the aphids and to prevent further insect infestation after the removal of the cages the plants were thoroughly dusted with derris powder. It has been subsequently discovered that derris may not give a 100% kill in the case of aphids. There is, therefore, the possibility that some escaped death. This may be an explanation of the results obtained.

Replicate I. All the plants which had been infested with the viruliferous aphids developed vine symptoms characteristic of leaf roll.

FIGURE X

Scale drawing of insect cage



The framework of scantling and lath was covered with a good grade of white cotton material

A - Side view

B - End view

C - Top view

The plants infested with the non-viruliferous aphids appeared normal. One of the control plants was slightly distorted.

Replicate II. The checks and all but one of the non-viruliferous, infested potato plants showed no signs of leaf roll. The viruliferous, infested plants all showed top distortion or rolling in the upper leaves. This may have been due to leaf roll, but symptoms were not definite enough to make a decisive determination possible.

Replicate III. The caged plants in this experiment, although somewhat rangy due to being covered, showed no other abnormalities. It is presumed that infection occurred too late to become outwardly manifest in the vines.

On February 21, 1945, all tubers were examined in storage for signs of phloem necrosis. The results are given in Table 15. Necrosis appeared in all experiments. The non-viruliferous groups exhibited a decreasing percentage of necrosis in each succeeding experiment, while the reverse was the case in the viruliferous groups. Necrosis also developed in the controls.

Table 15. Percentage of potato plants showing leaf-roll symptoms and hills with necrotic tubers.

Replicate number	Plants showing leaf-roll vine symptoms (16-9-1944)			Hills with necrotic tubers (21-2-1945)		
	Non-viruliferous	Viruliferous	Control	Non-viruliferous	Viruliferous	Control
	%	%	%	%	%	%
I	0	100	20	57	17	30
II	17	100	0	50	67	20
III	0	0	0	0	100	0

In these experiments necrosis of the phloem elements developed in the tubers of plants infested with the non-viruliferous population as well as in those having the viruliferous aphids. Thus, it must be assumed that, if the aphids used were initially virus-free, the aphids can, without the virus, initiate necrosis of the tuber phloem elements. This conclusion would be confirmed if these necrotic tubers produce healthy plants. If, however, they produce leaf-roll plants it must be concluded that, either the aphids were not virus-free, or that the plants became infested with viruliferous insects after the removal of the cages.

Consider this latter point. There are two possibilities. Some viruliferous individuals may have escaped and infested the controls and the other plants in spite of the fact that all plants, including the controls, were dusted thoroughly and regularly. As previously indicated, the derris dust may not have given a 100% kill, in which case some aphids may have survived. If this is true, the data in Table 15 may be misleading. There would be no proof that viruliferous aphids did not migrate considerably in the rows and infest the controls as well as the other potato plants, thus spreading the virus and initiating tuber phloem necrosis. There would be no proof that the aphids alone are responsible for this necrosis. Further experiments, using fumigation methods to give a definite 100% kill of the aphids, should be conducted.

The other possibility is that viruliferous aphids flew in from some adjoining field. Leaf roll was present in a field about 50 yards from the test plot. This field, although at a reasonably safe distance, can by no means be eliminated as a possible source of infection.

Tuber Graft Experiments

Schultz and Folsom (63) report the successful transmission of the leaf-roll virus by means of tuber grafts. They bound the cut halves of diseased and healthy tubers together with a rubber band.

In these experiments a piece of tissue from a diseased tuber was inserted into the healthy set at a point just below the eye. Wedge-shaped sections, approximately 1/2 inch wide, 1/2 inch long, and 1/8 inch thick, were cut from the leaf-roll infected tubers. These sections were always cut from the epidermis towards the centre of the tuber. In the healthy tuber a slit was made at a distance of about 3/8 inch below the eye and the diseased section inserted. All eyes not used were removed from the tuber. Grafted tubers were then cut into sets and these sets placed immediately in a cold room at the temperature of 38° F. They were planted in the field 24 hours later.

In September, 1944, six of the grafted plants showed signs of top distortion. This may have been due to leaf roll or possibly to other causes. The control plants appeared normal throughout the season; no necrosis developed in the tubers of these plants. On February 21, 1945, when the tubers from the grafted plants were examined, phloem necrosis was found in one case only. If the plants from these tubers should develop leaf roll under field conditions it will indicate that tuber grafting results in the transmission of leaf roll without the development of tuber phloem necrosis. That is to say, the leaf-roll virus itself may not be sufficient to initiate necrosis of the phloem elements.

Vine Graft Experiments

The plants to be grafted were grown in the greenhouse. When the grafts were made, all top growth was removed down to the first node above the soil surface. This left one simple leaf on a short main stalk. Immediately below the base of the petiole a slightly oblique slit, about one inch in length, was made in the stem. Into this slit a wedge-shaped piece of tissue from a diseased plant was inserted. These pieces were obtained from the petioles of infected plants by cutting off sections 1/2 inch in length. These were then sliced longitudinally to the desired thickness, the inner epidermis removed, and the section inserted into the slit in the healthy stem. The wound was then waxed and the plants placed in the shade at a temperature of about 70° F. They were allowed to remain in the shade for about five days before being transplanted into the field. There, fertilized and watered, they grew well and produced a fair yield of tubers.

The graft material used in these experiments was of the same stock as that on which the viruliferous aphids were raised. A field test on this material proved that it was severely infested with the leaf-roll virus.

A test lot consisted of twenty plants grafted as described. The healthy material used was tuber indexed, foundation stock of the variety Carter's Early Favorite. Grafts were made four times during the season, namely, June 27, July 3, July 18, and August 1. The plants were examined on September 20 for leaf roll. At this time some of the plants of the first and second lots showed signs of top distortion, and a slight rolling of the upper leaves. However, it could not be

definitely determined whether these symptoms were due to the leaf-roll virus or to some other cause. All lots were harvested on September 28 and the tubers stored in a root cellar. On February 21, 1945, these tubers were examined for phloem necrosis. The results are given in Table 16. However, these data are not final, since a later examination will be made and also plants will be raised from this stock to determine whether the virus was successfully transferred or not.

Table 16. Percentage of tuber phloem necrosis in vine-grafted material.

Lot	Percentage necrotic hills
1	15
2	30
3	5
4	0
Average	12.5

If these tubers should prove to be infected with leaf roll the results would seem to indicate that the leaf-roll virus, as transmitted by grafting, initiates tuber phloem necrosis. There is, however, the possibility that aphids, viruliferous or otherwise, from some nearby field, infested these plants. If such were the case it would be impossible to determine definitely the cause of the symptoms shown.

DISCUSSION

Survey

The results of the survey of five potato fields in the Edmonton district show that two aphid vectors of leaf roll, Myzus persicae and Macrosiphum solanifolii, are present. Of these, the latter is by far the more abundant. That both of these aphids are important in the spread of the leaf-roll virus at Edmonton is almost certain. However, a survey over a number of years is necessary before a definite statement can be made as to the relative prevalence of the various species and their seasonal abundance or importance in spreading the leaf-roll virus. The fact that M. persicae was more abundant in those fields showing the greatest amount of leaf roll is possibly only a coincidence, because it is unusual for leaf-roll symptoms to become definite until the following season.

The winter host of these two aphids is abundant in all parts of this country within easy flying distance of every potato field. Migrants can fly more than half a mile. It would be difficult to find any potato field in the Edmonton district a safe mile from a rose bush.

Weeds, such as lamb's quarter, which can serve as early hosts for these two aphids, are common throughout the district. The aphids can thus move by easy stages to the potato fields. Fields were probably not invaded to any extent until the latter part of June. As will be noted from Table 7, aphid populations were light even in mid-July.

Other insects, although very abundant in potato fields, do not appear to be of any importance as leaf-roll vectors. Yet it may be that some of them are able to initiate phloem necrosis in potato tubers.

Also, some experiments with Lygus elisus, the western tarnished plant bug, would be valuable. If this insect can carry the leaf-roll virus it would, because of its abundance and very wide host range, prove a very important vector in this district.

Field Experiments

Obviously the evidence from only one season's experiments cannot present conclusive evidence, and, therefore, more work is required.

Phloem necrosis developed in the tubers of those plants infested with the non-viruliferous aphids as well as in the tubers of those with the viruliferous population. If the aphids were initially virus-free the evidence indicates that the aphids can initiate this phloem necrosis without the leaf-roll virus. The occurrence of necrosis in the controls would then be due to accidental infestation by aphids or some other cause. Infestation of these plants by aphids may have resulted from migration from a nearby field or from the escape of a few aphids from the caged plants. If, however, the aphids were viruliferous, then there is no evidence that non-viruliferous aphids can cause tuber phloem necrosis. In this connection it should be mentioned that all plants, including the controls, were dusted before the cages were removed and that a careful examination of the plants indicated that the poisoning had been effective. However, if the derris did not kill all the aphids a mixed population of viruliferous and non-viruliferous individuals would have been free to move from plant to plant. If such were the case those plants which produced necrotic tubers may have done so because of leaf-roll infestation carried to them by viruliferous aphids. Naturally, final conclusions would not be reached without evidence from further experiments with new aphid populations.

It has been stated that tuber phloem necrosis is a symptom of the primary incidence of the leaf-roll virus. If non-viruliferous aphids could be shown to initiate phloem necrosis in plants having secondary leaf roll, the indication would be still stronger that the insects cause this necrosis.

No definite statement can be made in regard to the results of the grafting experiments conducted in 1944, because it will not be known until 1945, when plants are grown from this experimental material whether or not the virus was successfully transferred. The data in Table 16 show that 12.5 per cent of the vine-grafted potato plants produced necrotic tubers. If plants grown from this material develop leaf roll it would indicate that tuber phloem necrosis is initiated by the leaf-roll virus. However, since the plants were grown unprotected in the field, this relatively small percentage of necrosis may have resulted from accidental aphid infestation. If, when this experiment is repeated, no phloem necrosis develops in the tubers, the evidence may indicate that the necrosis is due to the aphid. However, even then such evidence may not be conclusive, because the amount of inoculum and the time of inoculation may be very important factors in the development of tuber phloem necrosis. Therefore, final conclusions cannot be reached until these factors have been given due consideration. On the other hand, the development of necrotic tubers by grafted plants, where aphid infestation is excluded, would strongly indicate that tuber phloem necrosis is a true symptom of primary leaf roll and independent of the insect vector.

SUMMARY

1. Literature dealing with the various aspects of leaf roll, its causal agent, and vectors, is voluminous. Considerable space is given to the review of this literature.
2. In a field survey conducted during the summer of 1944 two of the known aphid vectors of leaf roll, Myzus persicae and Macrosiphum solanifolii, were found to be present on potato plants in the Edmonton district. The latter is most abundant.
3. The wild rose, which may be an important winter host of these aphids, is common in the Edmonton district.
4. Field experiments in the transmission of the leaf-roll virus were conducted.
5. Necrosis developed in the tubers from those plants infested with non-viruliferous aphids, as well as in those plants infected with viruliferous aphids.
6. Twelve and one-half per cent of the vine grafted plants produced necrotic tubers.
7. Only one of the tuber grafter plants produced necrotic tubers.

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